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INHERITANCE OF RAMOSE INFLORESCENCE IN MAIZE.

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CONTENTS.

THE RAMOSE EAR VARIATION IN MAIZE.

From the standpoint of the origin of the ear of maize, perhaps the most instructive variation is the ramose type of inflorescence discovered by Gernert (4)[1] in a strain of Leaming Yellow Dent. In this variation the simple pistillate inflorescence is replaced by a compound structure which resembles somewhat the staminate inflorescence. Practically all the grain is borne on branches, the central axis bearing seeds at the extreme apex only. (Pl. I; see also Pl. X.) The larger surface on which seeds may be borne increases the potential production, although the actual yield of grain is much less than on normal plants of the parental variety. A single ramose ear has been found to produce 4,700 pistils (Pl. II), while the production of one-quarter of that number would be unusual on an ear of the parental Leaming variety. The failure to produce grain in quantity commensurate with the number of pistils seems to be due, at least in part, to the mechanical difficulty of exserting such a large number of pistils through the ends of the husks, although there doubtless are other restricting factors.

[1] Serial numbers in parentheses refer to " Literature cited " at the end of this bulletin.

While the pistillate inflorescence is entirely branched, none of the other characteristics of a normal ear are altered. The glumes are membranaceous and inconspicuous, the spikelets are paired and practically sessile, one flower only is developed in each spikelet, and there is no indication of the development of stamens. The branches bear four rows of spikelets, being similar in this respect to the branches of a tassel. The ramose ear, therefore, may be considered as a reversion to a more primitive type in only the one character of branching.

Accompanying the ramose pistillate inflorescence is an almost equally striking alteration in the form of the staminate inflorescence. (See Pl. XIII.) In normal maize the tassel has a few branches at the base and terminates in a single upright spike bearing four or more rows of paired spikelets. This terminal spike usually exceeds half the length of the entire inflorescence, and in some varieties its relative length is much greater. The transition from branches to a single central spike is abrupt, the upper and lower branches being of nearly the same length. In the ramose type of tassel the branching is continuous, extending from the base to within a few centimeters of the apex, leaving a very short central spike, while the total number of branches in extreme cases exceeds 400. These branches decrease gradually in length until they consist of but three or four spikelets on rather elongated pedicels, with an almost imperceptible transition from branches to pairs of spikelets.

As with the ramose ear, the tassels with their large number of branches produce a far larger number of spikelets than the tassels of commercial varieties, and also a greater amount of pollen. The whole tassel has a distinct conical shape quite unlike that of the normal form.

Since the ear of the Ramosa variety is branched in a manner similar to the tassel, with an absence of a predominating central spike, it would seem reasonable to conclude that the differentiation of the sexes in maize occurred before the loss of the lateral branches, and the central spike of the tassel may be assumed to have developed simultaneously with the single-spiked ear.

While the ramose type of inflorescence has been found to segregate as a unit in crosses with the normal form (1), no evidence has been presented to show whether this seemingly simple Mendelian character has suffered any alteration as a result of such hybridization and, further, whether the normal plants segregating from ramose hybrids have undergone changes in the structure of the inflorescence.

The opportunity to measure the effect of hybridization on Mendelian characters is unique in Ramosa × normal crosses. The ramose variation is large, affecting both staminate and pistillate inflores-

cences, and is readily classified qualitatively, while the component parts are numerous and subject to definite quantitative study.

DESCRIPTION OF THE PARENTS.

In the selection of a variety to cross with Ramosa, fortunately one was found which, in tassel dimensions, varies from the normal almost as much as the Ramosa, but in the opposite direction. The staminate inflorescence of this variety is of the familiar form, but it is extreme in having relatively few branches and a central spike which in some cases is half a meter in length (Pl. III). The pistillate inflorescence is normal, consisting of a single spike with 12 to 16 rows of seeds. This variety was collected by Dr. Palmer at Chihuahua, Mexico, and its native name Gordo has been retained.

Three crosses were made between the two types, Ramosa plants being used as female parents. These hybrids were designated Mh157, Mh158, and Mh159. A few first-generation plants were grown and self-pollinated, furnishing seed for the second generation. First-generation plants were grown again in larger numbers when the second-generation progenies were planted.

Fourteen characters were recorded for the second generation. These characters fall into two groups, those relating to the terminal staminate inflorescence and those relating to the pistillate inflorescence.

TASSEL GROUP.

Type of tassel: The tassels were classified into ramose or normal from their general appearance.

Length of the branching space: The length of the rachis in centimeters from the lowest tassel branch to the uppermost.

Length of the central spike: The length in centimeters of the single spike from the uppermost tassel branch to the tip of the spike. The combination of this measurement with that of the branching space gives the total length of the tassel.

Length of the uppermost tassel branch: The length in centimeters of the uppermost branch of the tassel. In ramose inflorescences it often is difficult to determine where the branches end and the pediceled spikelets begin.

Length of the lowest tassel branch: The length in centimeters of the lowest primary branch of the tassel.

Total number of branches: This measurement includes all primary and secondary branches as well as branches of a higher order.

Central spike index: The length of the central spike as a percentage of the total tassel length.

EAR GROUP.

Type of ear: Classified into ramose and normal from general appearance.

Number of branches: The number of branches on the ear. In typical ramose ears it is difficult to determine the total number of branches, since those at the apex are much subject to environmental influence. It has been the practice to record any ear with more than 50 branches as ramose.

Number of rows of spikelets on the terminal spike of the ear: This character corresponds to the number of rows on a normal ear, but on many ramose ears the terminal spike is so short and irregular that the number of rows can not be definitely determined.

Length of the terminal spike: The length in centimeters of the unbranched portion of the ear. This measurement corresponds to the length of the central spike of the tassel.

Terminal spike index: The length of the terminal spike as a percentage of the total length of the pistillate inflorescence.

Length of the entire ear: The length of the pistillate inflorescence in centimeters, including the branched and unbranched sections.

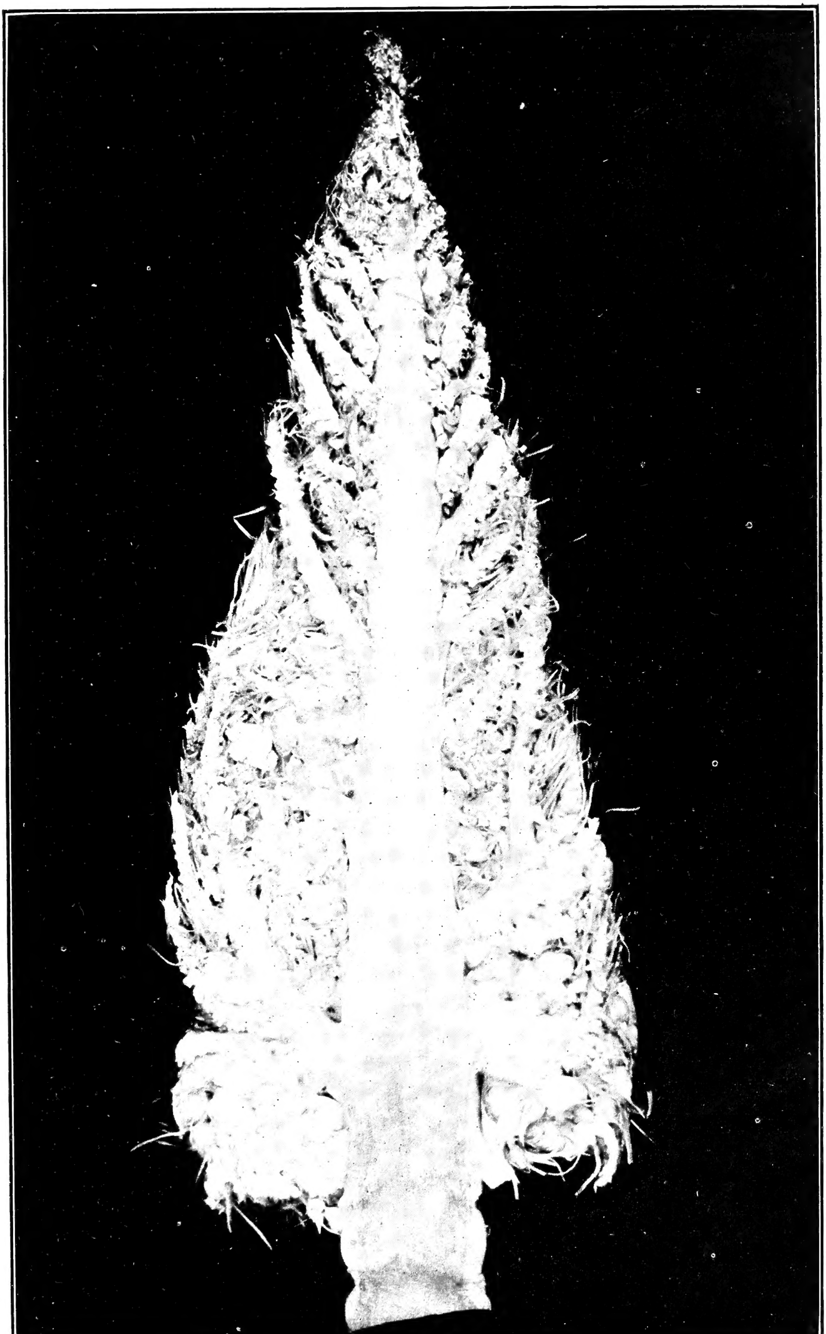
FIRST GENERATION.

The ramose characteristics of both pistillate and staminate inflorescences entirely disappeared in the first generation. This was in accordance with the results of other investigators as well as the previous experience of the writer.

Measurements of the several tassel dimensions, however, disclosed the fact that while the normal type of tassel, as represented by the Gordo variety, dominated the conical tassel of the Ramosa parent, nevertheless the Gordo type had undergone alteration, approaching more nearly the dimensions of the common maize tassel.

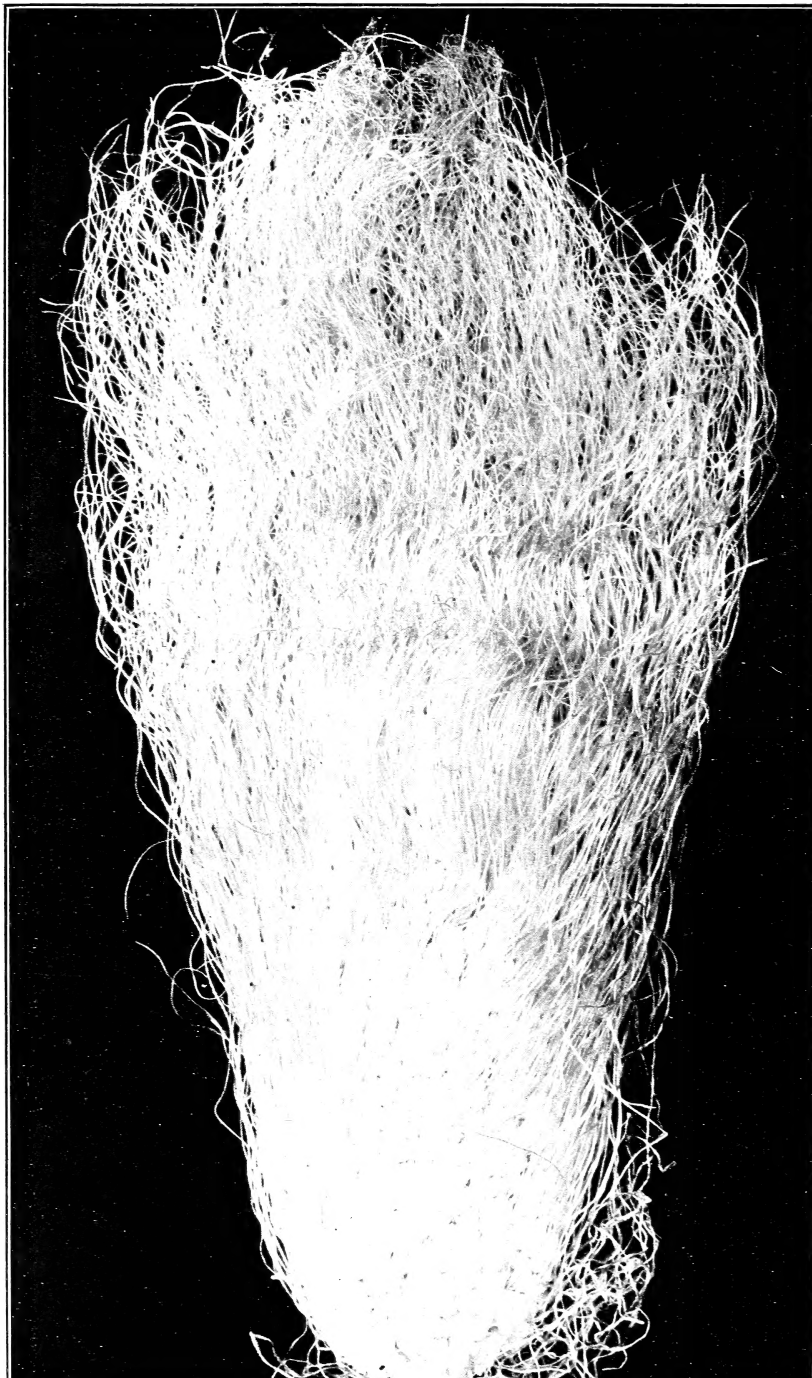
The vigor of the first generation was manifested in the size of the tassel, and the measurements of the several parts reflect this vigor. Thus, the length of the entire inflorescence exceeds that of the larger parent, and a subdivision of the inflorescence into the central spike and branching space shows that both of these parts have increased in length. This general increase in size prevents a direct comparison between the tassel dimensions of the F_1 and those of the parents, since the factor of heterosis can not be evaluated accurately. It would seem, however, that the length of the branching space, although less than the parental average, has been increased over that of the Gordo parent by a greater percentage than has the length of the central spike. This indicates the influence of the Ramosa parent, which would be expected to increase the length of the branching space at the expense of the length of the central spike.

A more direct measure of this effect is to be found in the central spike index. The index clearly shows that the proportion of rachis devoted to the production of branches has increased at the expense of the central spike, although the tassel is still of the normal type, the deviation toward the Ramosa parent being apparent only in the measurements. The measurements are given in Table I, and the frequency distribution of the central spike index are shown graphically in figure 1.



LONGITUDINAL SECTION OF A RAMOSE EAR OF MAIZE, SHOWING PROFUSE BRANCHING.

Such an ear when mature resembles that shown in Plate X. (Natural size.)

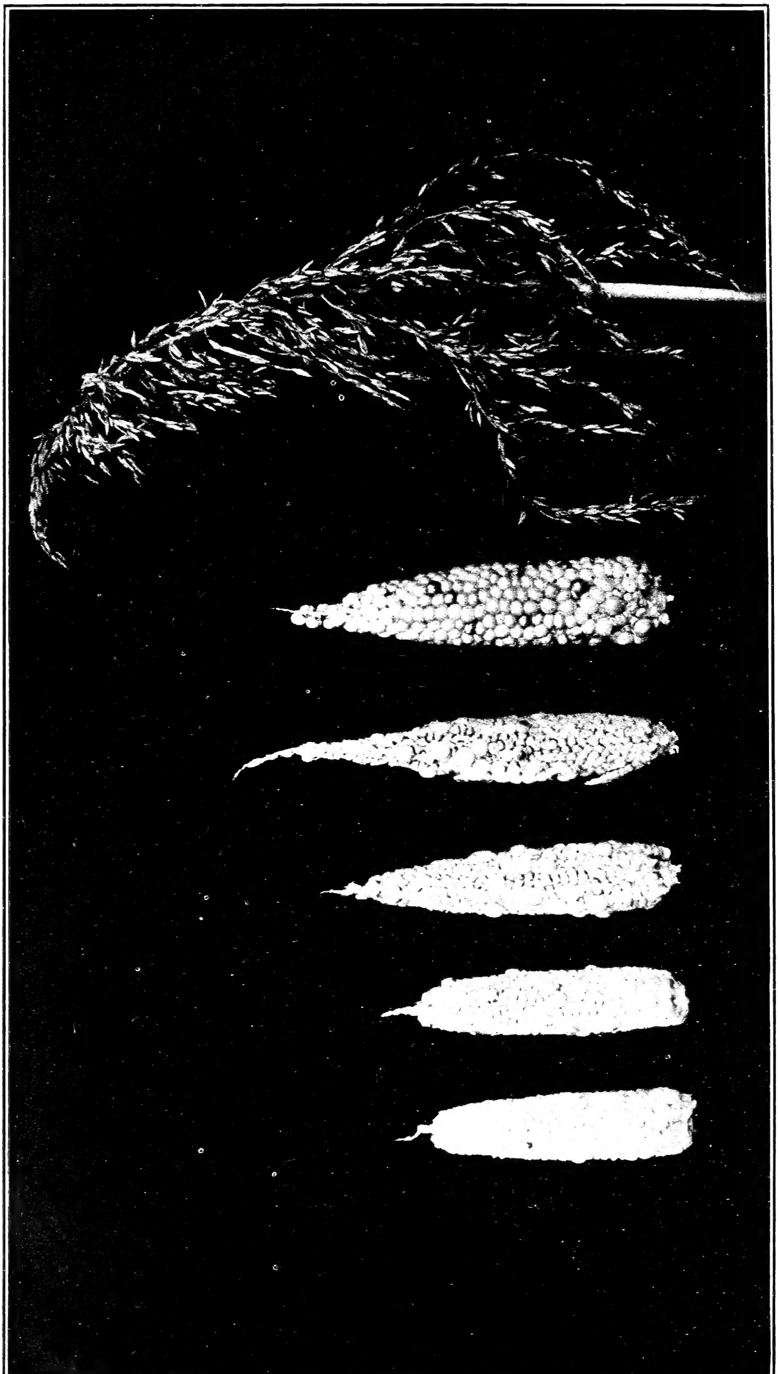


A RAMOSE EAR OF MAIZE, SHOWING PROFUSE SILKS.

The silks on this ear were determined by count to be 4,700. (Natural size.)

MAIZE PLANT, SHOWING THE TYPE OF TASSEL CHARACTERISTIC OF THE GORDO VARIETY.

The central spike of this tassel was 55 cm. long, while the spread from the tips of the branches was 80 cm.



TASSEL AND EARS FROM A SECOND-GENERATION PLANT OF A RAMOSA-GORDO MAIZE HYBRID.

The ear nearest the tassel is the uppermost, while the two farthest from the tassel were borne on tillers. Note the one small branch at the base of the second ear from the tassel.

SECOND GENERATION.

The ears of the first generation and, for that matter, the normal ears of the second generation provide no very good characters for a quantitative comparison with the parents, since the branches are suppressed. The plants of the second generation were grown from self-pollinated F_1 seed. No difficulty was encountered in classifying them as to their ramose or normal nature from the standpoint of the tassel, and although it was apparent that the ramose tassels were variable, the conical configuration left no ground for reasonable doubt. Both the normal and the ramose segregates of the second generation showed the effect of hybridization, behaving in a manner entirely comparable with that commonly expected in size characters (fig. 2). Although the normal and ramose segregates of the second generation were easily distinguished, it is apparent from the measurements in Table I that the tassels of the ramose plants are not, on the average, as ramose as those of the Ramosa parent, and likewise the tassels of the normal plants are not as extreme in form as those of the Gordo parent. This is shown graphically in the central spike index in figure 3. In each case the alterations are in the direction of the F_1. Thus the ramose character, while behaving in a general way as a unit in inheritance, is capable of being resolved into several parts which behave in inheritance as multiple-factor size characters (Table I). The counts, based on the configuration of the tassel, gave 130 ramose and 399 normal, or 24.6±1.3 per cent ramose.

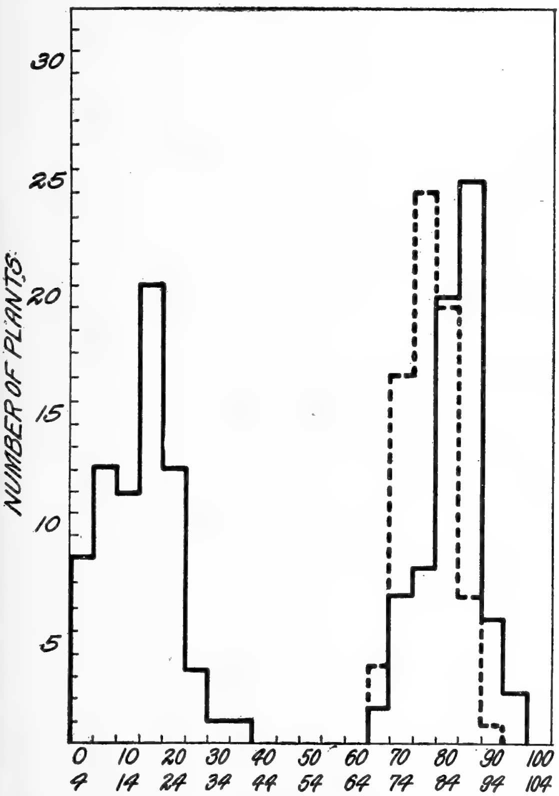


Fig. 1.—Frequency distributions with respect to the central spike index in maize plants of the Ramosa and Gordo varieties and of the first generation of this hybrid. Polygon at left, Ramosa; at right Gordo; inclosed in broken line, first-generation hybrid.

TABLE I.—*Measurements of the tassel characters of the Ramosa and Gordo varieties of maize compared with those of the first and second generations of their hybrids.*

Parental designation.	Measurements of length (centimeters).					Number of branches.	Central spike index.
	Entire.	Branching space.	Central spike.	Uppermost branch.	Lowest branch.		
Parents:							
Ramosa	32.6±0.37	27.7±0.32	5.0±0.23	1.8±0.05	20.7±0.31	133.7±3.69	15.5±0.58
Gordo	30.5±0.33	5.1±0.14	25.1±0.30	15.4±0.21	19.4±0.30	7.0±0.23	83.4±0.43
Combined F_1 [a]	47.7	10.7	36.7	21.8	28.0	14.4	77.6
Combined F_2:							
Normal [a]	38.4	8.3	30.0	17.3	22.3	13.4	77.4
Ramose [a]	33.5	21.7	10.3	3.1	17.6	58.9	30.8
Mh157 F_1	47.1±0.48	10.7±0.28	36.3±0.55	22.0±0.39	26.7±0.51	17.4±0.83	77.0±0.74
Mh158 F_1	48.6±0.33	10.8±0.16	37.6±0.28	22.2±0.26	28.4±0.30	11.8±0.30	77.7±0.30
Mh159 F_1	46.0±0.43	10.5±0.23	35.6±0.30	21.2±0.38	28.1±0.45	16.6±0.44	77.9±0.57
Mh157 F_2:							
Normal	33.7±0.27	8.4±0.12	24.9±0.21	14.8±0.18	18.4±0.24	19.2±0.35	73.6±0.33
Ramose	29.6±0.39	19.8±0.36	10.0±0.25	3.3±0.21	14.4±0.26	60.4±0.16	32.8±0.69
Mh158 F_2:							
Normal	40.3±0.39	8.0±0.26	32.4±0.55	18.3±0.46	23.4±0.55	10.0±0.37	80.1±0.62
Ramose	35.2±0.50	24.3±0.57	10.7±0.30	2.9±0.11	18.6±0.46	55.2±1.51	30.5±0.79
Mh159 F_2:							
Normal	43.2±0.39	8.6±0.21	34.5±0.37	19.5±0.28	27.3±0.44	10.3±0.32	78.7±0.45
Ramose	38.1±0.66	28.2±0.62	10.0±0.60	3.4±0.20	22.8±0.72	66.0±0.70	25.3±1.24

[a] The several progenies were combined for purposes of inspection only, and therefore the probable errors were not calculated. As a close inspection of the table will show, sister progenies differed in some characters by amounts too large to be ascribed to chance, and therefore the combined progenies do not constitute a homogeneous population.

When the ears were harvested the variability in the expression of the ramose character was even more striking. Plants classified as ramose from the characteristics of their tassels bore ears which ranged in a continuous series from unbranched cobs to the typical ramified inflorescence (fig. 4). The unbranched ear produced on a ramose plant is shown in Plates IV and V, while some of the intermediate stages are shown

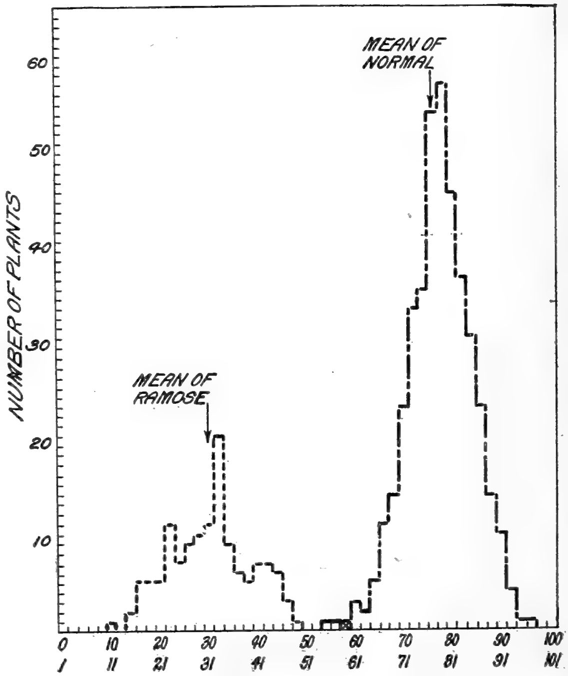


FIG. 2.—Frequency distributions with respect to the central spike index in maize plants of the second hybrid generation of Ramosa-Gordo. The square marked with a cross represents a plant classed as ramose.

in comparison with a typical ramose ear in Plates VI to X. This series could be expanded by the addition of still other intermediate ears, but it is believed that these are enough to show the degree of variability.

CORRELATION OF THE EAR CHARACTERS OF THE SECOND GENERATION.

The correlations of the ear characters with the tassel characters for these F_2 segregates have been calculated and are summarized in Table II. The highest correlation found between the 5-ear and 4-tassel characters is that of 0.546 between the total number of branches on the ear and the same character of the tassel. The next highest correlation is —0.406 between the number of branches in the tassel and the terminal spike index of the ear. This index is in a sense complementary to the number of branches on the ear, the correlation between these two characters being —0.642.

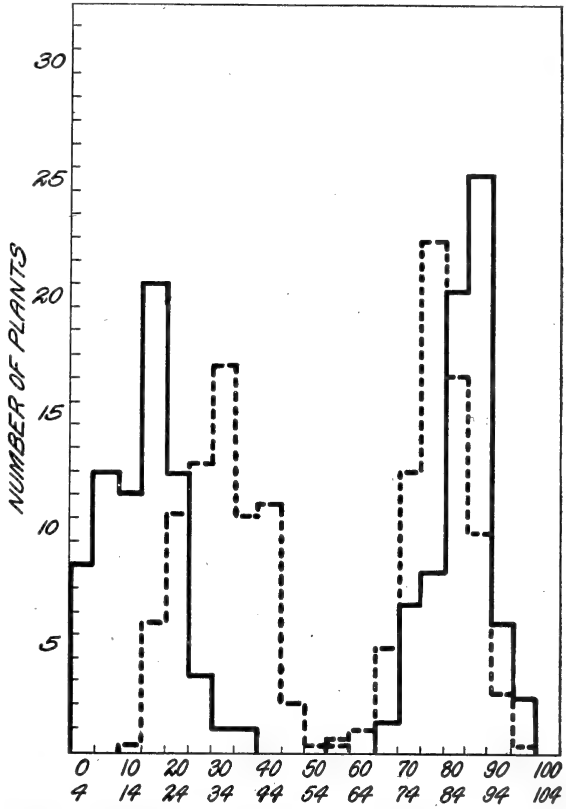


FIG. 3.—Frequency distributions with respect to the central spike index in maize plants of the Ramosa and Gordo varieties and of the normal and ramose segregates of their second-generation hybrids. Polygons inclosed in solid lines: At left, Ramosa; at right, Gordo. Polygons inclosed in dotted lines: At left, ramose segregates; at right, normal segregates. The populations of Gordo and of the normal and ramose segregates have been plotted on the basis of 69 individuals, to facilitate comparison with Ramosa.

The only other significant correlation which does not comprise a measure of the number of tassel branches as one character is a rather unexpected correlation of 0.398 between the lengths of pistillate and staminate inflorescences, which may be an indication of general vigor.

Among the ear characters the only significant correlations obtained which are not explained readily as being measures of the same characteristics are the coefficients of 0.756 between the number of

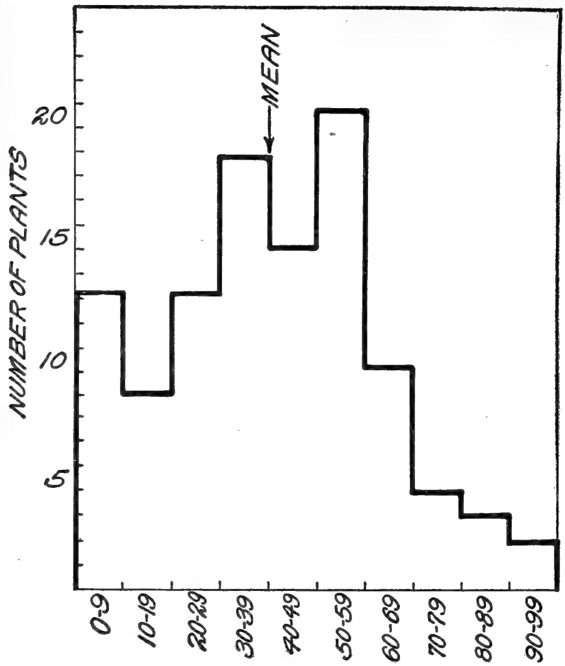


FIG. 4.—Frequency distributions with respect to the number of branches on the ear in plants of the second-generation ramose segregates of Ramosa-Gordo maize hybrids.

rows and the length of the ear spike and —0.472 between the total number of branches and the number of rows. Both coefficients indicate that as the central axis approaches a normal ear in length it also resembles a normal ear in the number of rows.

Among the tassel characters no correlations are found which are not capable of obvious explanation. Thus big tassels have long central spikes, while the longer the central spikes the fewer the branches.

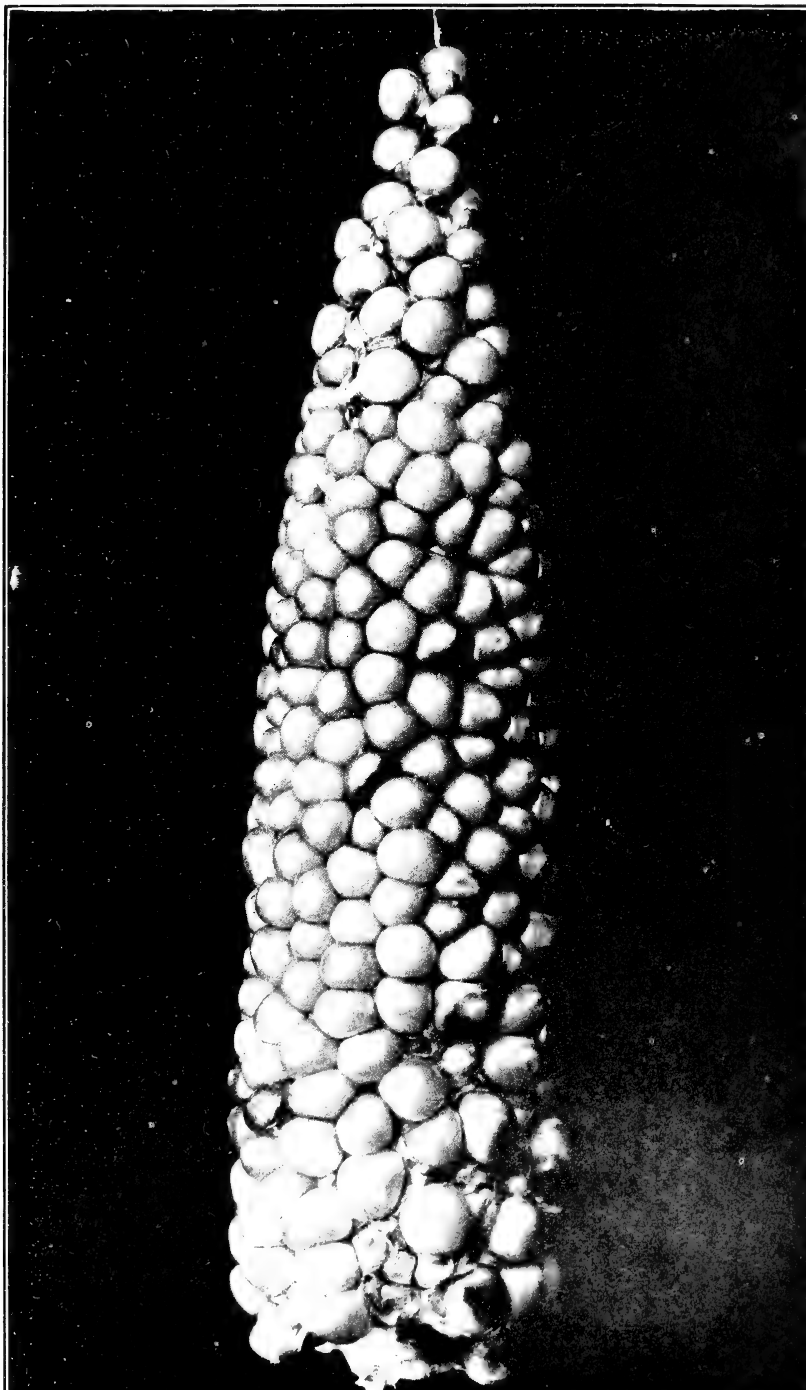
TABLE II.—*Summary of the correlations between the ear and tassel characters in the second generation of Ramosa-Gordo maize hybrids.*

[The population for which these coefficients were calculated consists of 102 individuals. Any coefficient greater than 0.196 exceeds three times the probable error.]

Character designation.	Branches on ear.	Number of rows on the central spike of the ear.	Length of terminal spike of the ear.	Length of the entire ear.	Ear spike index.	Length of tassel.	Length of the central spike of the tassel.	Number of branches in the tassel.	Central spike index.
Branches on ear	....	−0.472	−0.596	0.235	−0.642	0.055	−0.237	0.546	−0.291
Number of rows on the central spike of the ear	−0.472	....	.756	.300	.745	.147	.192	−.308	.156
Length of the terminal spike of the ear	−.596	.756	....	.391	.946	.163	.241	−.393	.154
Length of the entire ear	.235	.300	.391	....	.179	.398	.147	.035	−.103
Ear spike index	−.642	.745	.946	.179	....	.134	.212	−.406	.152
Length of tassel	.055	.147	.163	.398	.134	....	.407	.123	−.115
Length of the central spike of the tassel	−.237	.192	.241	.147	.212	.407	....	−.409	.811
Number of branches in the tassel	.546	−.308	−.393	.035	−.406	.123	−.409	....	−.503
Central spike index	−.291	.156	.154	−.103	.152	−.115	.811	−.503	....

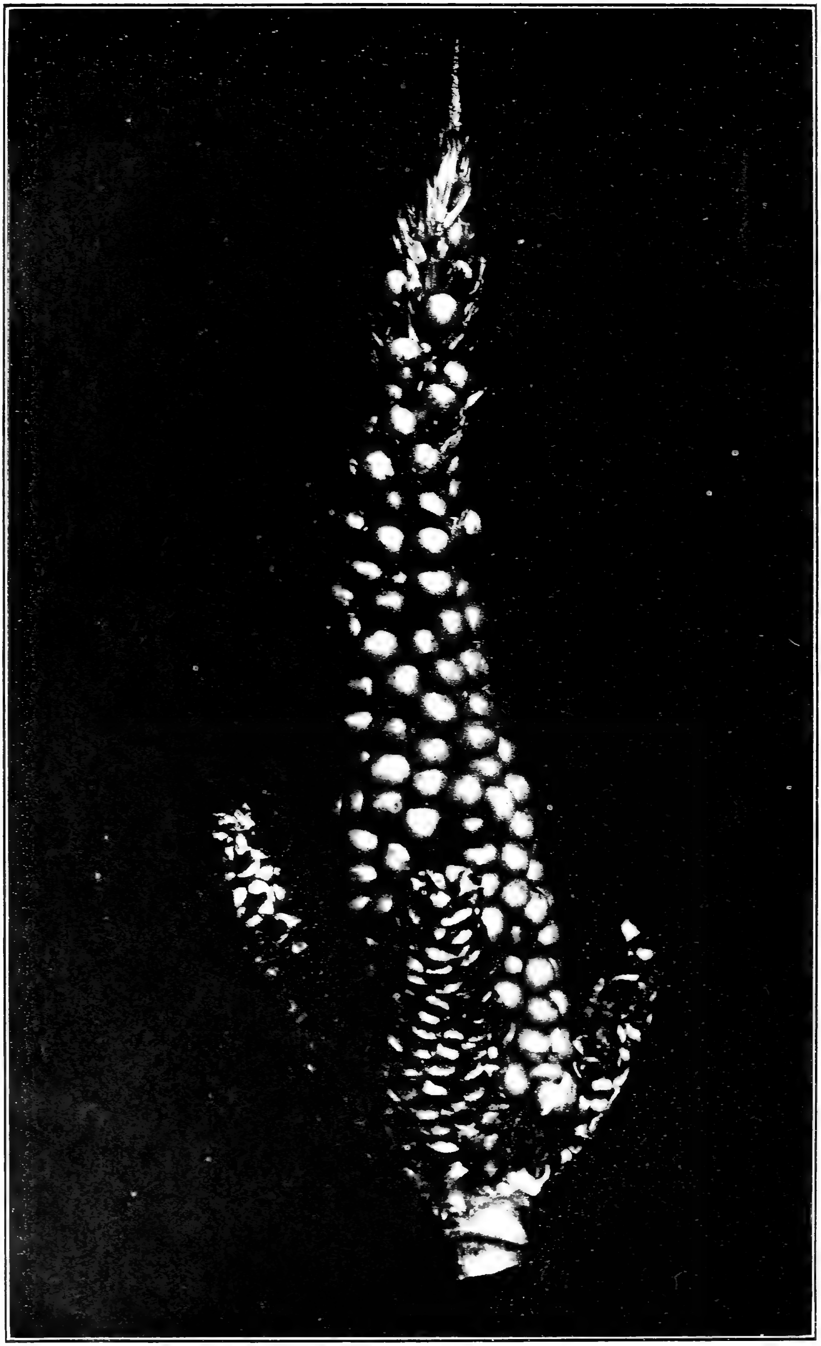
THIRD GENERATION.

The appearance at harvest of markedly intermediate ears associated with intermediate tassels indicated that intermediate forms



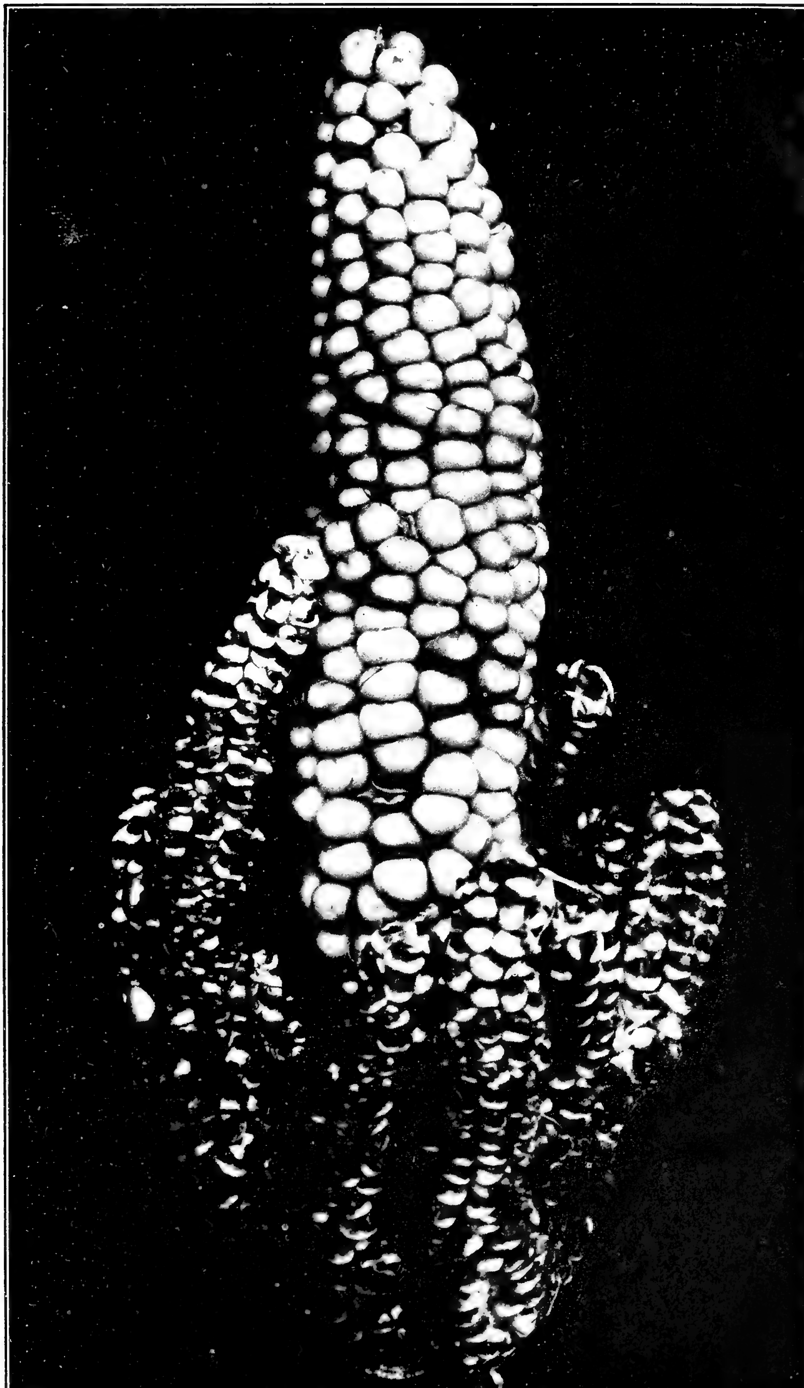
AN UNBRANCHED EAR OF THE SECOND GENERATION OF A RAMOSA-GORDO MAIZE HYBRID.

The tassel of the plant which bore this ear was classified as ramose. (Natural size.)



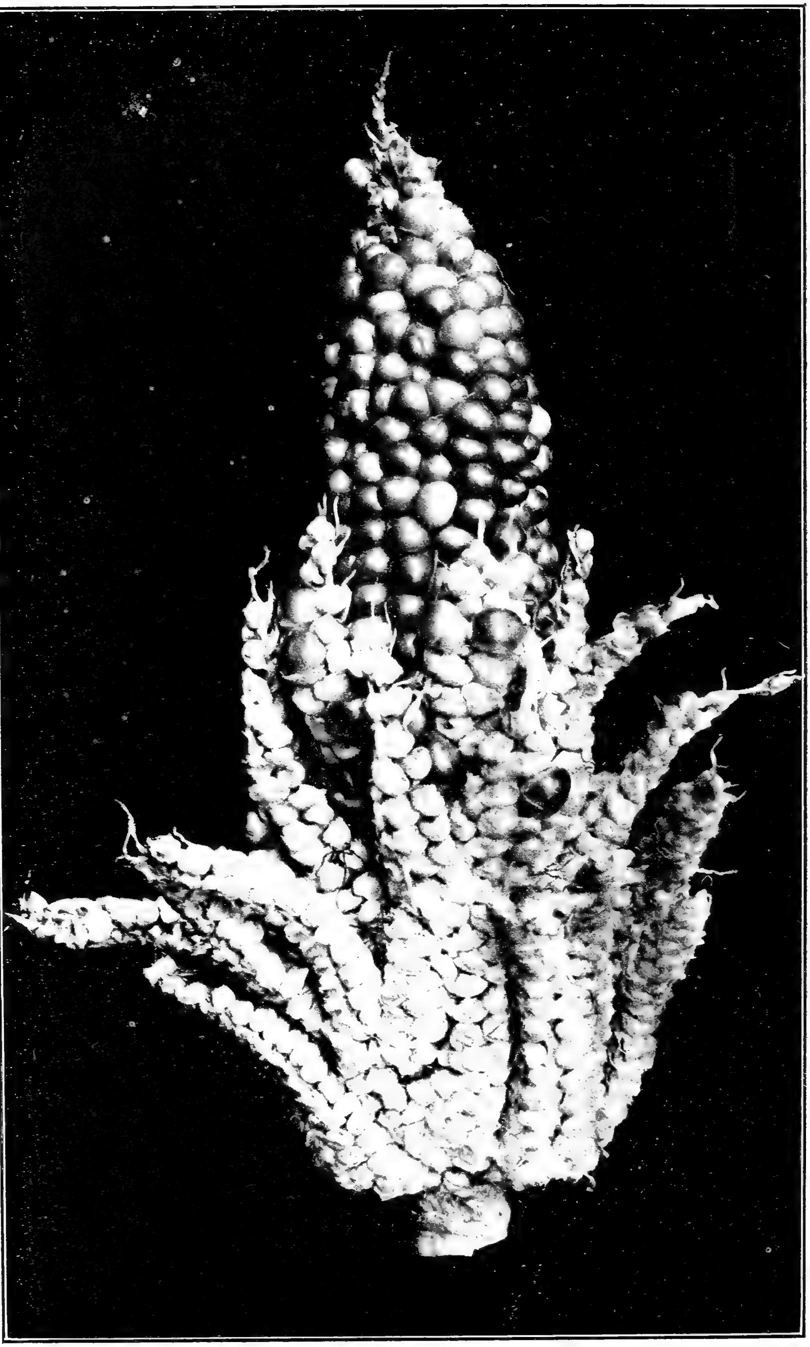
AN INTERMEDIATE RAMOSE EAR FROM THE SECOND GENERATION OF A RAMOSA-GORDO MAIZE HYBRID.

There is a gradual loss in the number of rows of spikelets from the base to the tip. The branches on this ear have eight rows of spikelets. (Natural size.)



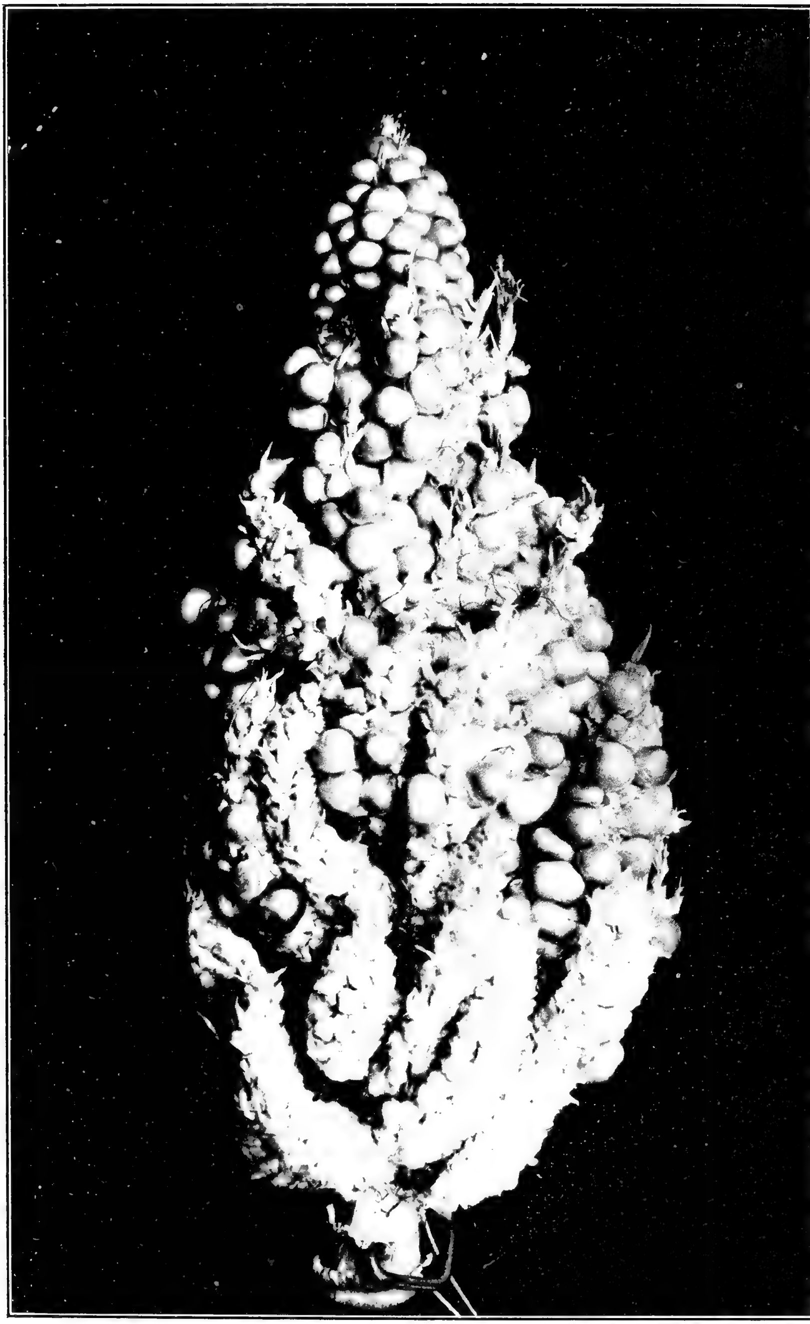
AN INTERMEDIATE RAMOSE EAR OF MAIZE WITH WELL-DEVELOPED CENTRAL AXIS.

The branches on this ear have eight rows of spikelets. (Natural size.)



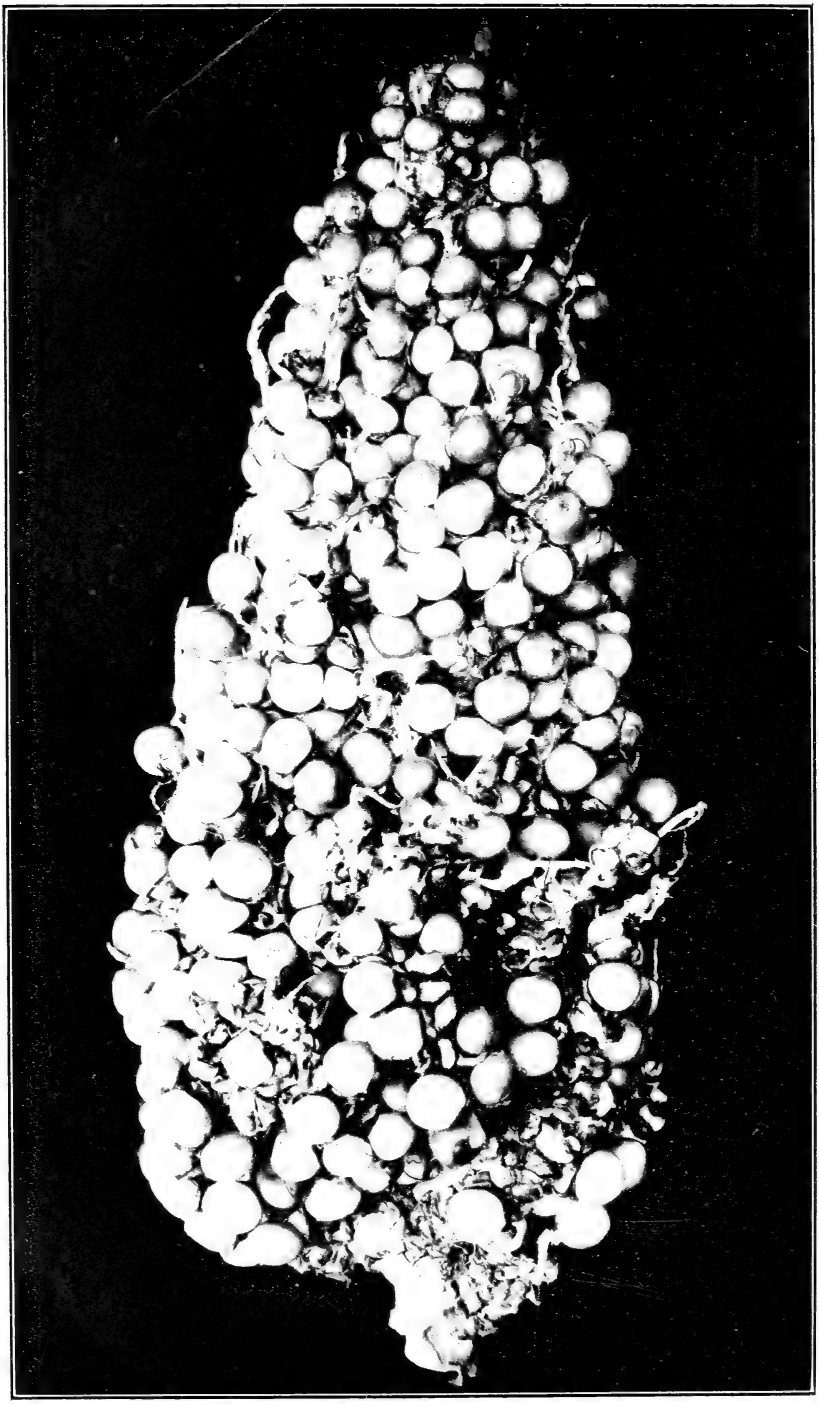
AN INTERMEDIATE RAMOSE EAR FROM THE SECOND GENERATION OF A RAMOSA-GORDO MAIZE HYBRID.

Compare with Plate X. (Natural size.)



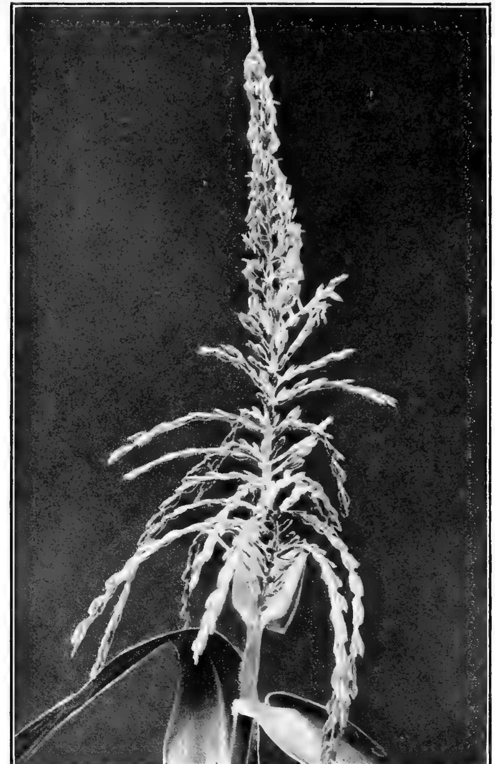
AN EAR PRODUCED IN THE SECOND GENERATION OF THE RAMOSA-GORDO MAIZE HYBRID.

The development of branches here shown is not much inferior to a typical ramose ear. (Natural size.)



A TYPICAL RAMOSE EAR OF MAIZE, SHOWING THE ARRANGEMENT OF THE SEEDS.

(Natural size.)



TWO FORMS OF INTERMEDIATE RAMOSE TASSELS FOUND IN THE FOURTH GENERATION OF A RAMOSA-GORDO MAIZE HYBRID.

The tassel at the left is typical of several progenies. Neither plant had branches on the ears.

SECTION OF THE CENTRAL SPIKE OF THE TASSEL FROM A PLANT OF THE THIRD GENERATION OF A RAMOSA-GORDO MAIZE HYBRID.

The spike here shown is of an intermediate ramose type. (Natural size.)

of the ramose character could be established. Since no further generations were contemplated at the time of flowering, none of the second-generation plants was hand-pollinated. In order to test the possibility of isolating intermediate strains, two open-pollinated ears were saved for planting. Both ears were grown from and had a preponderance of white seeds, indicating that little cross-pollination had taken place, since most of the adjacent sister progenies were producing yellow seeds. One ear was unbranched and the other had only four basal branches, but both were from plants which produced obviously intermediate ramose tassels, as is shown in Table III in comparison with the tassel measurement of their Ramosa parent.

TABLE III.—*Tassel measurements of the Ramosa parent compared with those of two plants having branched and normal ears selected from the third generation of maize hybrids.*

Form of ear.	Measurements of length (centimeters).				Number of branches.	Central spike index.
	Branching space.	Central spike.	Uppermost branch.	Lowest branch.		
Ramose	27.7	5	1.8	20.7	133.7	15.5
Unbranched	29	7	3	24	68	19
4-branched	20	11	3	22	63	35

From the unbranched ear 23 plants were raised, 13 of which produced ears with branches ranging in number from 2 to 35, but none approaching a typical ramose ear. These branched ears, as well as some of the unbranched ones, were produced by plants that had tassels intermediate between normal and ramose. Some of the plants with unbranched ears obviously were hybrids with normal plants, but the ears of others could be classed definitely as resembling the parental unbranched ear.

Grown as progeny of the 4-branched ear were 19 plants, and of these 7 were branched, 1 being a good ramose, while the other 6 had from 3 to 15 branches. In this progeny, as in the other, tassels intermediate between ramose and normal were found.

FOURTH GENERATION.

Of the 42 plants in the third-generation progenies, 18 were self-pollinated and progenies were grown from them. These 18 plants varied in the number of branches on the ear from none to a typical ramose inflorescence. All of the plants showed unmistakable signs of their Ramosa ancestry in the form of the tassel (Pl. XI). The measurements of the F_4 plants are given in Table IV.

TABLE IV.—*Comparison of the staminate and pistillate inflorescences of the fourth generation of the Ramosa-Gordo maize hybrid Mh158.*

Parental designation.	Measurements of tassel length (centimeters).					Number of branches.		Central spike index.
	Entire	Branching space.	Central spike.	Uppermost branch.	Lowest branch.	Tassel.	Ear.	
L2L1L1	37.6±0.64	20.2±0.41	17.4±0.59	4.6±0.18	26.3±0.60	43.4±1.27	3.5±0.62	45.6±1.14
L2L1L2	41.6±0.79	20.7±0.56	20.8±0.87	6.9±0.53	23.6±0.64	23.2±1.5	0	49.6±1.9
L2L1L3	41.1±0.80	24.7±0.63	16.1±0.66	5.3±0.21	25.8±0.63	48.4±2.1	5.5±0.65	39.0±1.18
L2L1L4	34.3±0.58	15.8±0.58	18.7±0.51	5.1±0.28	21.5±0.52	23.0±1.35	0	54.7±1.36
L2L1L5	35.5±0.60	21.9±0.31	13.5±0.53	4.4±0.26	17.3±0.58	41.2±1.12	.3	37.6±0.97
L2L1L6	41.4±0.72	17.5±0.66	23.9±0.66	8.4±0.55	28.2±0.58	22.2±1.46	0	57.8±1.43
L2L1L7	31.5±0.71	22.2±0.53	9.2±0.41	3.2±0.69	16.8±0.64	48.3±1.66	14.1±5.84	29.2±1.37
L2L1L8	37.5±0.52	25.3±0.47	12.0±0.50	4.1±0.20	21.0±0.61	54.2±1.90	9.5±1.05	32.0±1.16
L2L1L9	32.5±0.55	21.5±0.45	11.0±0.42	4.0±0.19	16.0±0.50	41.7±1.47	4.5±0.87	33.7±1.06
L2L1L11	35.2±0.62	19.6±0.53	15.6±0.44	5.8±0.33	17.6±1.44	39.2±1.32	7.9±1.19	44.4±1.13
L2L1L12	37.9±0.69	22.2±0.74	15.6±0.69	5.4±0.28	23.8±0.65	36.0±1.70	2.3±0.62	41.1±1.68
L2L2L1	40.8±0.67	15.7±0.69	25.1±1.13	13.4±0.88	24.2±0.93	32.2±1.67	....	60.0±2.12
L2L2L2	32.7±1.10	17.7±0.72	14.6±1.12	5.2±0.37	14.4±0.58	30.2±1.53	3.9±0.89	43.9±1.48
L2L2L3	33.0±0.92	22.4±0.68	10.4±0.63	5.5±0.41	18.5±0.35	52.3±1.93	11.2±1.06	30.9±1.51
L2L2L4	31.0±0.63	17.9±0.49	13.0±0.68	4.2±0.14	18.0±0.60	50.4±2.13	....	41.3±1.40
L2L2L5	29.4±0.75	15.5±0.37	13.9±0.53	4.5±0.24	16.8±0.42	25.2±1.06	.6	47.0±1.26
L2L2L6	26.7±0.89	12.5±1.04	14.2±0.80	4.5±0.29	13.4±0.53	22.3±2.16	3.6	53.6±2.53

The distribution of the F_2, F_3, and the F_4 plants for branches on the ear is shown in Table V, and the distribution for the branches on the tassel in Table VI. The number of branches on the ear is the best single quantitative expression for the degree of branching, although subject to a certain variation due to variation in the size of the whole inflorescence.

In Table VI the positions of the parent plants are shown by plus marks. The positions of plants which bore ramose ears are shown by italic figures; where there were two such plants only one of them bore a ramose ear except in a single instance (marked with a star at line 54, column 38) wherein two plants bore ramose ears.

In the tassels of the F_4 the difficulty of giving a single expression for the degree of branching is much greater. This may be due to the larger size of the staminate inflorescence, which tends to emphasize the variability by magnifying small differences. The total number of tassel branches is, of course, reduced on plants of low vigor, and in a general way this may be reflected in a reduction in the size of the entire inflorescence, though the correlation between the size of the tassel and the number of branches in the ramose segregates of the F_2 is but 0.123 ± 0.066. The best indication of the ramose character is the general form of the inflorescence, which is difficult to reduce to a single expression. Thus, in one F_4 progeny many of the plants developed in addition to the usual basal branches one or two branches midway in what otherwise was a normal central spike (Pl. XII). In some of these plants also the pedicels of the paired spikelets gradually increased in length toward the base of the central spike, giving this organ a pronounced conical shape (Pl. XI). Neither the num-

ber of branches, the length of the branching space, nor the central spike index would measure properly such behavior, as all would approximate closely the dimensions of a normal tassel.

TABLE V.—*Distribution of plants of the second, third, and fourth generations of the Ramosa-Gordo maize hybrid Mh158 for the number of branches in the ear.*

[The distribution in the second generation is for ramose plants only. The position of the parental ear is indicated either by italic figures or by a plus mark. R indicates ears classed as ramose, since the number of branches exceeded 50.]

Branches per ear.	Progeny distribution differentiated by parents (number of plants).																				
	L2 F2.	L2L2F3.	L2L2L1 to 6 F4.						L2L1F3.	L2L1L1 to 11 F4.											
		4	0	3	7	9	15	R	0	0	0	0	0	0	3	3	4	5	11	17
0	1	12	*16*	1	15	2		4	*10*	*26*	*22*	*23*	*9*	*1*	23	2		8	2	2
1				1	2	1		2				2	2	2				4	2	
2	1				2	2		2	1			3	1	2		4			4	
3	3	1		+	1	2	1	2	3				3		+	+	2	1	1	1
4	3		1	1	1		3	1	3				1	1		2	*3*		1	
5				1			1	1	2							1	2	*2*	1	
6		1		1		1	1	1					1			2	2	1	1	1
7		1			+	1	1							2		2	2		1	
8	2					2							1			2		1		1
9	2	1				+								1			2	1		1
10		1		1			1										2	1		
11	1						2		1					1					+	
12	1								1								4			
13							2							1						
14							1												1	
15	1	1					+							1		2	1			
16	1						1	2									1	2		
17	1								1				1							+
18	1						1						1	1						
19	2																			
21	2													1						1
22	2																	2		1
23	2																			
24	1			1			1													
25	1																			
26	2																			
27	1						1													
29	1																			
30	5																			
32	2																			
33	3																			
35	3								1											
36	2																			
38	1																1			
39	2																			
40	2																			
41	1																			
42	1																			
43	3																			
44	2																			
45	1																			
46	1																			
47	1																			
48	1																			
49	1																			
50	3																			
R	35	1	4	1		1	2	*1*						3				5	2	12

The F_4 progenies demonstrate the possibility of isolating true-breeding intermediate forms, though the progenies differed among themselves in the degree of branching, viewed either from the standpoint of the tassel or from that of the ear. Nine of the progenies produced some plants with typical ramose ears, one progeny having as many as 12 plants with ramose ears in a population of 20.

Although this same progeny also had a relatively large number of tassel branches, it was exceeded in this character by four other progenies. Two progenies produced a total of 48 plants, all with unbranched ears, though both progenies bore unmistakable evidences of their Ramosa ancestry, possibly most marked in the staminate inflorescence, but apparent also in the form of the ears. It seems not unreasonable to predict that subsequent generations of these two progenies will continue to produce unbranched ears, though a relatively few plants with poorly developed ear branches may be expected for a few generations. It is difficult to believe that these progenies will ever give rise to typical ramose ears.

A typical ramose ear was produced on a plant that had but 32 tassel branches with a central spike index of 47, while an unbranched ear was borne on a plant with 57 tassel branches and having a central spike index of but 39. Thus, it is seen that extreme branching of one inflorescence is not associated inseparably with an extreme condition in the other, although in Gernert's original mutation the ramose characteristics of both inflorescences invariably appear together.

TABLE VI.—*Distribution of plants of the second, third, and fourth generations of the Ramosa-Gordo maize hybrid Mh158 for the number of branches in the tassel.*

Tassel branches.	Progeny distribution differentiated by parents (number of plants).																			
	L2F₂.	L2L2F₃.	L2L2L1 to 6 F₄.						L2L1F₃.	L2L1L1 to 11 F₄.										
		49	7	12	16	25	37	44	68	23	35	36	38	48	54	78	82	87	97	?
3														1						
5								1												
6		1							1											
7		3	+																	
8														1						
9											1			1						
10								1			1									
11		1			1					4				2						
12		2		+						1	3									
13		1			1			1		2					1					
14		1						1	1	2	2									
15	1																			1
16	1	1			+1		1	1		2				1						
17				2				2						2						
18		1			1			1	1		1									
19		2			1				1	1	1			4	1					
20					2		1	1		1	1	1		3						3
21				1						1	1									
22					3		2			2	2			1				1		
23				2	1		1	1	1	+								1		1
24	1			3		1				1		1				1	1			1
25		1			1	+	2	1			1			1						
26				3	1			1			1				1					2
27			1	1			1			1										
28			1	2	1	1		1		1	1			1	1		2		1	1
29				1	1		1			2						1	1	1	1	2
30												1	1		1		1			
31				1	3						1								1	1
32					2						1	*2*	*1*						1	1
33	1		1		1	3	1					1	*1*	3	1	1		1	1	1
34							1								1		1			1
35	2			1	1				1	1	+1	1	1			1		1		2
36		2		1			1		1			+	1		1			1	2	
37	1	1					+								1			1		1
38	1								1	1			+		2	1		1		

A TYPICAL RAMOSE TASSEL OF MAIZE.

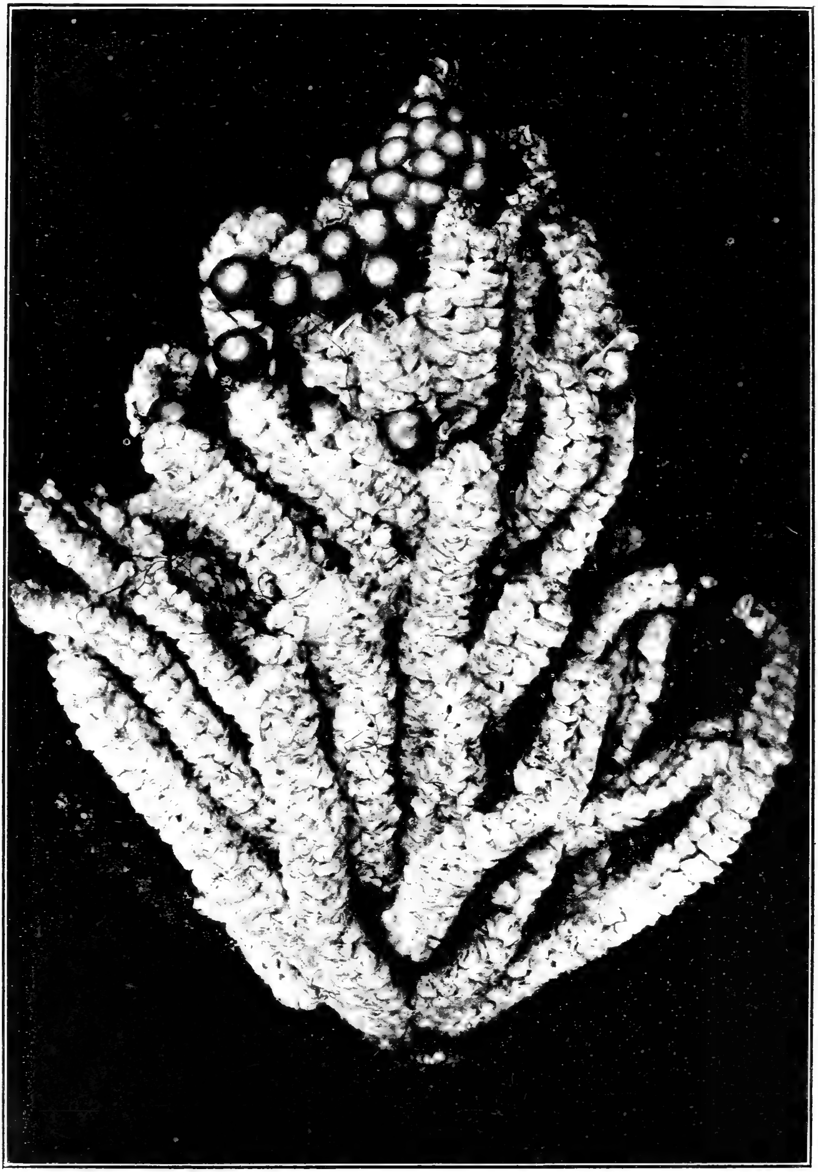
This tassel is from a plant of Mr. Mack's Yellow Evergreen variety. Compare with Plate XIV, showing an intermediate form.

AN INTERMEDIATE RAMOSE TASSEL FROM MR. MACK'S SWEET-CORN VARIETY.

Compare with Plate XIII, showing a typical ramose tassel.

TWO BRANCHED EARS OF MAIZE.

The ear at the left is from the second generation of a Ramosa-Gordo hybrid, while that at the right is from a nonramose stock from the Pawnee Indians. (Natural size.)



AN INTERMEDIATE RAMOSE EAR FROM THE SECOND GENERATION OF A RAMOSA-GORDO MAIZE HYBRID.

The long branches shown have 8 and 10 rows of spikelets. (Slightly reduced.)

TABLE VI.—*Distribution of plants, etc.*—Continued.

Tassel branches.	Progeny distribution differentiated by parents (number of plants).																			
	L2F₂.	L2L2F₃.	L2L2L1 to 6 F₄.						L2L1F₃.	L2L1L1 to 11 F₄.										
		49	7	12	16	25	37	44	68	23	35	36	38	48	54	78	82	87	97	?
39	1	1					*2*			1				1			1	4		
40	2			*2*	1	1					1	2			4			3	1	
41	1		1	1								3	1			1		1	1	
42	3			1		1				1					1	2		1	2	1
43						1				1	1			1	*1*		3		1	1
44	1	1						+				*2*				1		1	2	1
45	1					1						1	1		3		1	1	1	1
46							1	*1*		1	1	1				1	1	1	2	1
47	1		2						1			*2*	*2*	1					*1*	
48	2	1	1			1	1		1			1		+	2	1	1		1	
49	2	+	2	1											1	1	2	2	2	
50	2		1	*1*					1				2		1			1		
51	2																1			1
52	2											1	1		1		1	1	1	
53	1		1			1			1				1					1		
54	4		1						1				*		+*1*	2	1			
55																	1		1	
56	2												1		1		1	1	1	1
57	2		2			1		1										1		1
58			1			1			1				1		1	2			1	
59	1	1	2													1	1			
60	1												1				1			
61	2		1												*1*	1				1
62						1							2						*1*	
63	3					1			1				1				2			
64	1					1									1				1	
65	1																			
67						1											1			
68	1		*1*						+											
69	1												1							
70			1			1														1
71	1																1			
72	1															1				
73	1																1			
75						*1*														
76	1			*1*					1											
77	1																			
78									1							+				
81						1														
82	2								1							1	+			
83			1																	
85	1																			
87									2									+		
93	1																			
96									1											
97	2								1										+	
110									1											

DISCUSSION.

The simple Mendelian behavior of the ramose character in the earlier experiments indicated that the present unbranched form of pistillate inflorescence and the reduced number of branches in the staminate inflorescence were the result of a single major genetic change. The variability of the ramose segregates from the Ramosa-Gordo hybrids indicates that the evolution of the ear from a branched inflorescence was a gradual process. That the branching tendency of the staminate and pistillate inflorescences can be separated indicates that the two inflorescences did not undergo change at the same time, and from the general absence of branches on ears it would seem reasonable to infer that the transformation from

branches to spikelets first took place on the lateral inflorescences, the terminal inflorescences undergoing alteration later. However, it can not be stated definitely that the reduction of branches of the staminate and pistillate inflorescences is due to completely independent genetic changes. The fact that the ramose variation as found had both inflorescences much branched and that they remain closely associated in most hybrids is an argument in favor of the hypothesis that the type of branching is constitutional with the plant and not restricted to particular inflorescences. If this were true, the ability to produce a highly ramified pistillate inflorescence on a plant with but little more than a normal number of branches in the staminate inflorescence would be attributed to genetic changes that have taken place since the original suppression of branches.

In this connection it is of interest to note the experience of Mr. J. M. Mack, of Fall Brook, Calif., who for 11 years has been unsuccessfully attempting to eliminate the ramose type of ear from a variety of sweet corn. The ramose variation made its appearance in

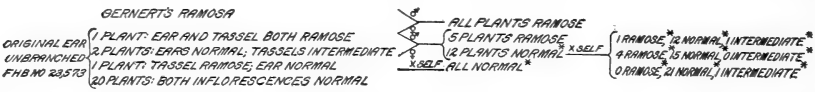


FIG. 5.—Diagram showing the pedigree of Mack's Yellow Evergreen sweet corn. Classifications marked with an asterisk (*) are based on the ear characteristics; most of the normal plants had intermediate tassels.

Mr. Mack's stock in 1909, three years before its discovery by Gernert. Undoubtedly both strains originated independently, though crosses have proved them to be genetically identical. The seed of this sweet corn, used in experiments by the Office of Acclimatization and Adaptation of Crop Plants, was received from the Office of Seed and Plant Introduction, United States Department of Agriculture, FHB No. 23573, in March, 1917. Some of the plants grown from the seed in 1918 were found to have typical ramose tassels (Pl. XIII), while others showed a well-marked intermediate stage (Pl. XIV), the whole progeny with respect to the tassel falling into three fairly distinct groups of 17 normal, 2 intermediates, and 2 ramose. When the ears were harvested it was found that none of the intermediate or normal plants bore branched ears, and only one of the ramose plants bore a branched ear, but this was a typical ramose ear. The ears borne on the plants with intermediate ramose tassels showed no indication of the ramose character, the rows being regular, the pedicels short, and the ears only moderately tapered. The intermediate tassels differ from those developed in the Ramosa-Gordo hybrids in that the only trace of Ramosa is the short central spike accompanied by the rather large number of branches (Pl. XIV).

It was found on a visit to Mr. Mack's gardens that the ramose plants were not being recognized until the ears were harvested. Thus, no selection was exercised against the ramose form of tassel except in so far as the two forms of inflorescence were associated. The result appears to have been an unintentional separation of the ramose ear from the characteristic ramose tassel. Even after 11 years of selection ramose ears appear occasionally and in combination with ramose tassels, but many more plants with typical ramose tassels and unbranched ears are found. The most common type of plant has a perfectly normal ear, while the tassel is intermediate between normal and ramose. Several self-pollinated progenies have been grown from these typical plants, and their pedigree is shown in figure 5. In a population of 55 plants, 5 produced typically ramose ears while 2 bore ears with branches only at the base—1 with an 8-rowed branch, the other with the common 4-rowed branches. Thus, in the apparently normal ears the ramose tendency may be manifested slightly. These branched ears have little in common with the branched ears developed in the Ramosa-Gordo hybrid, as they depart from the normal unbranched form only by the few branches. They resemble more closely a type of branching found in the Pawnee variety, and frequently in other varieties, the resemblance being so close as to suggest a relationship. The branched form of the Pawnee has remained unstable through three generations of self-fertilization, although the percentage of branched-ear plants has increased. The small number of branched ears in these intermediate strains of Mr. Mack's sweet corn seem to offer an entirely parallel case, and it may be justifiable to conclude that the Pawnee type of branched ear is simply a reduced stage of the ramose form.

Whether the intermediate forms of Ramosa isolated from the Ramosa-Gordo hybrid represent a series of multiple allelomorphs, multiple factors, or modifying factors remains an unsolved problem. The intermediate forms seem to be recessive to the typical Ramosa; at least a cross between a plant having an ear with 17 branches and a typical ramose plant gave fully ramose plants in the first generation. On the other hand, the progeny of the self-pollinated intermediate parent produced 11 ramose, 6 intermediate, and 2 unbranched ears. Results of this kind are disconcerting from the standpoint of simple analysis. About the only conclusion possible at this time is that true-breeding intermediate strains have been isolated having unbranched ears.

While many ears without branches are produced by the plants of the Ramosa-Gordo hybrids, they nevertheless exhibit other characteristics of their Ramosa ancestry which become more evident with a study of the intermediate forms. The seeds are borne on pedicels much longer than those of normal ears, and the abrupt taper with

the irregular rows is another indicative characteristic. The shape of these unbranched F_2 ears and also of many of the F_3 and F_4 intermediates strongly suggests the ears of a variety from the Canary Islands, the tassels of which have been noted as suggesting Ramosa. Other ears with 3 to 10 branches, similar to those found in Mr. Mack's variety, resemble the branched-ear variation of the Pawnee variety (Pl. XV). A similar type of branching has been found in the Texas Surcropper variety by Mr. W. W. Ballard and in the California Yellow Flint by Mr. C. G. Marshall. However, in these forms of branched ears from other than Ramosa stocks none has been found that had more than 4 rows of seeds on the branches, while on many of the Ramosa segregates the number of rows of spikelets on the basal branches is frequently 8 and sometimes as many as 10 (Pl. XVI). The gradation from typical ramose ears to ears without branches affords evidence for the reduced-branched theory of the origin of the many-rowed cob (2), although in many of the ears the rows are extremely irregular and the abrupt taper from base to tip, with the consequent continuous reduction in the number of rows, militates against the development of the common cylindrical ear. Indeed, a study of these ears raises a serious doubt as to the possibility of developing our present regular-rowed ears through a reduction of lateral branches to pairs of spikelets. In many instances the intermediate ramose ears clearly show that the branches reduce to a single spikelet instead of a pair, and in consequence each alveolus has but one seed; while the irregularity of the whole rachis precludes the possibility of determining accurately the number of rows, it is apparent that such ears could have an odd number of rows. The origin of the original ramose variation in the Leaming variety is of interest in this connection, since one of the most constant characteristics of the Leaming variety is the poorly formed tip, which in many ears appears to have been artificially joined to the main portion.

It is difficult to visualize the common ear of maize as having arisen through the reduction of the branches of the inflorescences as they are now constituted, since there is little regularity in their present arrangement. If the branches of a normal maize tassel were reduced to paired spikelets, these spikelets would be arranged in a very irregular manner on the rachis and would bear little resemblance to the regular-rowed ears. If the reduction is assumed to have occurred at an earlier period when the branches of the inflorescence had a distichous arrangement similar to the present arrangement of the vegetative branches, the resulting ear would have but four rows, and the problem of their increase to the present number remains.

Hackel has explained the increase in the number of rows as the result of a coalescence of 4-rowed branches, a theory supported by numerous bifurcated and bear's-foot ears. Collins (3), in studying teosinte-

maize hybrids, found evidence that the number of rows was increased through a twisting of the rachis. Hackel's hypothesis of coalescence does not account for the arrangement of branches on the staminate and pistillate inflorescences of either ramose or normal plants. The Ramosa-Gordo hybrids furnish evidence that the present type of inflorescence developed through the reduction of branches which presumably occurred subsequent to the twisting of the rachis.

It is difficult, however, to account for the present complete differentiation of branching space and central spike in the staminate inflorescence on the theory of reduced branches, since it necessitates the assumption that the reduction ceased abruptly at about the midpoint of the staminate inflorescence, while it continued to the base of the pistillate inflorescence.

The frequent appearance of branched but nonramose ears where the pistillate inflorescence is more nearly of the form of the common staminate inflorescence strongly suggests that the loss of the basal branches followed rather than preceded the separation of the sexes.

If the view is adopted that the many-rowed spikes originated through the reduction of branches, it must be concluded that this reduction took place in two distinct periods. Thus, the upper two-thirds of the spike was developed through branch reduction, resulting in an inflorescence with a central spike and basal branches, a condition which was stabilized in the staminate inflorescences, while in the pistillate inflorescences the remaining basal branches have been reduced to spikelets or possibly entirely aborted. With this idea of the reduction of branches in restricted areas, it becomes possible to explain the bifurcated or bear's-foot ears by assuming that the reduction in branches began somewhat below the apex at a point corresponding to the place where the staminate spikelets first open. The branches above this point were reduced later, and the bear's-foot ear is a variation entirely comparable with the development of basal branches. In this connection it may be more than a coincidence that the branched-ear variation in Pawnee appeared simultaneously with a distinct bifurcation at the apex representing a reversion to the condition suggested in this hypothesis that the central section of the branches were the first to be reduced. In other words, the reduction in branches first took place on a central section of the rachis, leaving the tip and base branched, though the apical branches, of course, were short. These two sections were reduced later, and from the frequency of their reappearance it may be not unreasonable to infer that the branches of the tip were the last to go. On the other hand, if the change in the form of the pistillate inflorescence was entirely similar to that of the staminate inflorescence, the order of the disappearance of the branches must be reversed, since the basal branches of the staminate inflorescence have yet to be reduced except in the

most extreme form of the hairy Esperanza variety, where the tassel consists of a single spike having many rows of clustered spikelets.

The reduction of the branches of the staminate inflorescence involved only those branches that were finally eliminated, while the others remained unaltered. Thus, there was no general shortening of all the branches, resulting in the complete reduction of the short upper branches, but rather a definite change from branches to spikelets in the upper portion. This is illustrated in figure 6, where it is seen that the form of the present normal inflorescence would be almost exactly that of the ramose inflorescence if the upper branches of the ramose inflorescence were reduced without altering the re-

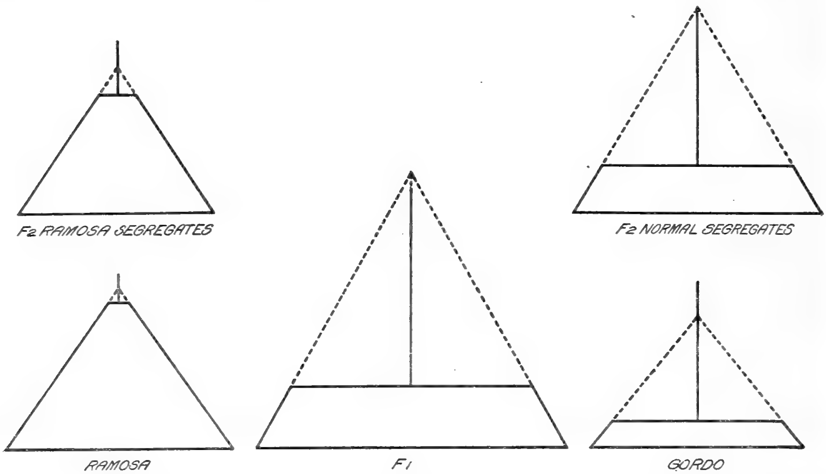


FIG. 6.—Diagrams showing tassel configurations of the first-generation plants and the normal and ramose segregates of the second-generation plants of Ramosa-Gordo maize hybrids. The solid vertical line represents in each diagram the length of the central spike, while the horizontal lines show the length of the lowest and the uppermost branches. The dotted lines show the projected angles formed by the lowest and uppermost branches.

maining branches, while it is equally apparent that the central spike of the Gordo variety has been elongated.

CONCLUSIONS.

The branched-ear variation designated *Zea ramosa* by Gernert has behaved generally as a simple Mendelian character recessive to the normal condition. In Gernert's variation the number of branches in the staminate inflorescence are increased greatly, and the configuration of the inflorescence is altered. This characteristic staminate inflorescence has always appeared in conjunction with the ramose ear, enabling the observer to detect the Ramosa plants in the field before examining the ears.

Crosses have been made between this ramose type and a type of maize from Mexico called Gordo, which has very few tassel branches,

departing from the common form in the opposite direction from that of the ramose variation.

Although in a general way the Gordo type of staminate inflorescence is dominant to the ramose form in the first generation of the hybrid, the influence of the Ramosa parent can be detected easily when the various parts of the inflorescences are measured. The ears of the F_1 were normal and without branches.

In the second generation of these hybrids the plants segregated into normal and ramose plants. Classified from the general appearance of the tassel, approximately one-fourth of the plants were ramose, supporting the results of previous investigations. Measurements of the various parts of the tassel showed, however, that the ramose segregates had undergone alterations, having retained partially the characteristics of the Gordo parent, while conversely the normal plants showed the effect of their Ramosa ancestry.

In the ramose group the general appearance of the tassels showed great variability. When the ears were harvested a similar range was observed. Plants classed as ramose from the characteristics of the tassel had ears without branches, although the converse of this was not observed. Ears were obtained which ranged in an unbroken series from typical ramose to those without branches. In a general way these intermediate forms of ears were associated with a similar intermediate condition of the tassel. An F_3 was grown from two open-pollinated ears, one without branches and the other with but four branches, both having tassels which betrayed their Ramosa parentage. The progeny of these plants ranged from typical ramose to normal in respect to the ears, although most of the tassels were intermediate between ramose and normal.

Eighteen F_4 progenies were grown from self-pollinated F_3 plants and showed that the diversity observed in the second and third generations was inherited. Two of the progenies produced only ears without branches, but the Ramosa ancestry was apparent in the tassels. These two progenies were both from unbranched ears. On the other hand, the progeny of a self-pollinated ramose ear produced 1 typically ramose, 11 intermediate, and 4 unbranched ears. It remains to be determined whether the modification of the ramose variation is the result of introducing numerous modifying factors through the Gordo parent, or whether the ramose character depends upon the combination of multiple factors for intense expression, or whether the true-breeding intermediate forms represent a series of multiple allelomorphs.

During the course of these experiments another ramose variation has been found which is genetically identical with Gernert's variation, but this appeared three years earlier in the gardens of Mr. J. M. Mack, at Fall Brook, Calif. In this strain an intermediate

ramose condition is common, and occasionally plants have the typical ramose staminate inflorescences in combination with normal unbranched ears.

The appearance and behavior in inheritance of the intermediate ramose plants suggest a relationship with branched forms from non-ramose stocks and furnish evidences for the development of the single-spiked ear through a reduction of branches.

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